

The road to oblivion – quantifying pathways in the decline of large old trees

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ABSTRACT

Large old hollow-bearing trees have a wide range of key ecological roles in forest and other ecosystems globally. Patterns and rates of mortality and decay of these trees had profound effects on the size and composition of their populations. Using an 18-year empirical study of large old trees in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, we sought to determine if there are particular patterns of decline that are shared by a proportion of the trees in a tree population. We also sought to identify drivers of decline of these trees by quantifying relationships between the condition state of trees (*viz*: tree form) and a range of covariates.

We found that time, stand age and fire can individually and in combination, strongly affect the decay (and eventual collapse) of large old trees. In particular, we found compelling evidence that patterns of tree decline were markedly different in old growth forest (stands dating from ~ 1850) relative to three other younger age classes examined. Trees in older forest decayed less rapidly than trees of equivalent tree form in younger forest. Old growth stands also were characterized by trees in an overall much lower (more intact) form category than the other age classes of forest. A key pattern in our study was the rapid deterioration of large old trees in the youngest aged stands (*viz*: those regenerating after fires in 1939 and following disturbance between 1960 and 1990). In these forests, a very high proportion of large old trees were either in the most advanced state of tree decay (form 8) or had collapsed (form 9). This is a major concern given that 98.8% of the Mountain Ash forest ecosystem supports forest belonging to these (or even younger) age cohorts. Our investigation highlights the need for forest management to: (1) increase levels of protection for all existing large old hollow-bearing trees, (2) expand the protection of existing regrowth forest so there is the potential to significantly expand the currently very limited areas of remaining old growth forest.

INTRODUCTION

Large old trees are keystone structures in many forested, agricultural and urban ecosystems worldwide (Manning *et al.*, 2006; Moga *et al.*, 2016; Lindenmayer and Laurance, 2017). These trees have many ecological roles including habitat provision for wildlife (Fischer and McClelland, 1983; Rose *et al.*, 2001; Lindenmayer and Laurance, 2017), acting as a source of fallen coarse woody debris on the forest floor (Elton, 1966; Maser and Trappe, 1984), and affecting nutrient cycles (including storing large amounts of carbon) (Keith *et al.*, 2009). In common with the populations dynamics of all long-lived organisms, rates and patterns of mortality of adult trees strongly affects the size and long-term dynamics of populations of large old trees (Gibbons *et al.*, 2008). Indeed, high levels of adult mortality is one of the key factors underpinning elevated rates of decline of large old trees in many ecosystems globally (Lindenmayer *et al.*, 2012).

Trees can pass through a range of morphological stages over their lifespan and after they have died. A range of decay classes has been identified for large old trees in several forest types such as the Douglas Fir (*Pseudotsuga menziesii*) forests of north-western North America (e.g. Cline *et al.*, 1980), the wet ash eucalypt forests of south-eastern Australia (Lindenmayer *et al.*, 2016) the boreal forests of Canada (Burton *et al.*, 2003) and oak forests of eastern Europe (Moga *et al.*, 2016). These stages correspond to trees in a sequence of conditional states from intact living trees to dead collapsed trees (Keen, 1955; Cline *et al.*, 1980; Lindenmayer *et al.*, 2016). The progression of trees through these stages is probabilistic with any given tree not necessarily passing through all decay classes; for example, a living intact tree may not undergo any deterioration (such as becoming a dead standing tree), but rather collapse directly to the forest floor. Given such probabilistic changes, two key inter-related questions are:

Are there particular patterns of change in condition that trees follow through the process of decay and collapse? That is, are there particular patterns of change shared by a proportion of the trees in a tree population? If so, are these patterns influenced by the age of forest in which trees are located and/or whether the stands have been affected by disturbances such as fire?

For this investigation, we sought to answer these questions for the iconic Australian tree, Mountain Ash (*Eucalyptus regnans*) which is the tallest flowering plant on earth. Large old trees in these forests are important nesting sites for a wide range of cavity-dependent vertebrates (Lindenmayer *et al.*, 2017) and understanding their patterns of decline is critical for predicting temporal changes in biodiversity, including for a range of threatened species such as the Critically Endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) and the Vulnerable greater glider (*Petauroides volans*) and yellow-bellied glider (*Petaurus australis*) (Lindenmayer *et al.*, 2015). Large old trees are also store large amounts of carbon (Keith *et al.*, 2009; Keith *et al.*, 2017) and well as influence the water cycle in Mountain Ash forests (Vertessy *et al.*, 2001). Quantifying the pathways of decline and the factors influencing the pattern of occurrence of large old trees is therefore important to better inform how to best manage populations of these keystone structures. Moreover, the approach we have employed to model pathways of decline in cohorts of large old trees has potential application in other kinds of forests, particularly those in places like western North America and boreal forest environments where such trees are critical for an array of cavity-using taxa (e.g. see Rose *et al.*, 2001; Franklin *et al.*, 2002; Burton *et al.*, 2003).

98 **METHODS**

99 *Study area and surveys of large old trees*

100 We completed this study in the Central Highlands of Victoria, south-eastern Australia
 101 where there is approximately 157 000 ha of Mountain Ash (Keith *et al.*, 2017). The primary
 102 form of natural disturbance in this forest is high-severity, stand-replacing or partial stand-
 103 replacing wildfire; the last major conflagration was in 2009 when 78 300 ha of Mountain Ash
 104 burned (Berry *et al.*, 2015). In addition, approximately 80% of the Mountain Ash forest estate
 105 in the Central Highlands is located in areas broadly designated for wood production and the
 106 predominant silvicultural system is clearcutting in which cutblocks of 15-40 ha are harvested
 107 (Flint and Fagg, 2007).

108 We established 96 long-term ecological research sites in Mountain Ash forest. Each site
 109 was 1 ha in size, on which we completed repeated measurements of the number and condition
 110 of large old hollow-bearing trees over an 18-year period between 1997 and 2015. We mapped
 111 and marked all 534 large old hollow-bearing trees with permanent metal tags and unique
 112 identifying numbers to facilitate re-measurement.

113 We used maps of past disturbances, together with on-ground reconnaissance of field
 114 sites (where tree diameter is strongly correlated to tree age; (see Lindenmayer *et al.*, 2017) to
 115 assign each of our 96 sites to one of four distinct age classes. These were: **(1)** stands that
 116 regenerated after a wildfire in approximately 1850, **(2)** stands that regenerated after a major
 117 wildfire in 1939, **(3)** stands that regenerated after fire or logging between 1960 and 1990, and
 118 **(4)** mixed-aged stands that comprised trees from 1730-1850 and a younger-aged cohort
 119 (typically regeneration from the 1939 fire).

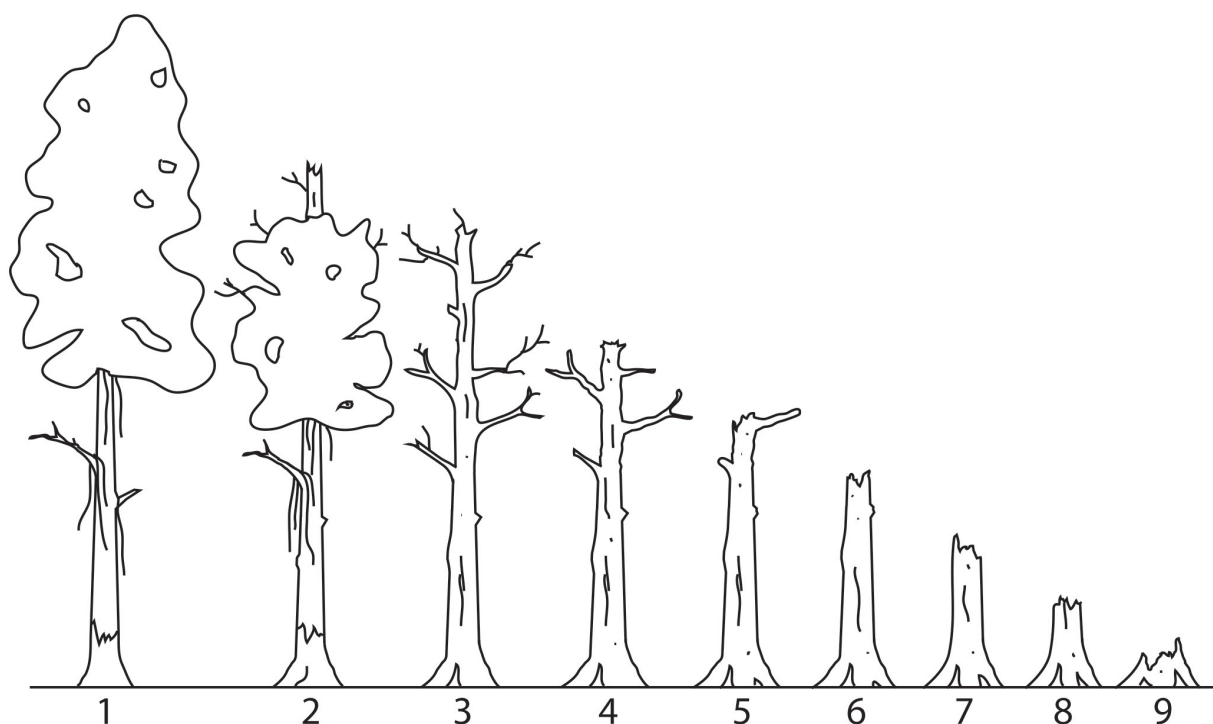
120 None of our long-term sites was subject to logging over the duration of this study (*viz*:
 121 1997 to 2015). However, parts of the surrounding area of approximately half our sites were

subject to timber harvesting between 1950 and 2015, with an average of 16.9% of the adjacent area logged up until 2015.

Classification of trees into different states of decay

For the purposes of this study, we defined a large old hollow-bearing tree as any tree (live or dead) measuring > 0.5 m dbh and containing an obvious cavity as determined from careful visual inspection using a pair of binoculars. We classified all large old hollow-bearing trees on our long-term sites into one of nine forms based on the condition and level of decay (Figure 1). Notably, all large old hollow-bearing trees were standing living or dead at the outset of our study in 1997.

Figure 1. Nine forms of decayed trees in the Mountain Ash forests of the Central Highlands of Victoria. Form 1: Ecologically mature, living tree with apical dominance; Form 2: Mature living trees with a dead or broken top; Form 3: Dead tree with most branches still intact; Form 4: Dead tree with 0–25% of the top broken off; branches remaining as stubs only; Form 5: Dead tree with top 25–50% broken away; Form 6: Dead tree with top 50–75% broken away; Form 7: Solid dead tree with 75% of the top broken away; Form 8: Hollow stump. Form 9: Collapsed tree.



Covariates used in statistical analysis

We fitted five potential explanatory variables to our models. These were: (1) year, (2) the age of the stand in which a given site was located, (3) whether a site had been burned in the 2009 fire, (4) the amount of forest burned in 2009 in a 2 km radius circle around the centroid of each site (weighted by the distance from the site centroid), and (5) the amount of forest logged between 1950 and 2015 in a 2 km radius circle around the centroid of each site (weighted by the distance from the site centroid).

STATISTICAL ANALYSIS

We fit a Bayesian multi-level model to tree form, with two random effects: site and tree. The site level random effect allowed for correlation among trees at a given site and the tree random effect allowed for temporal correlation. We assumed a Gaussian distribution for tree form. However, due to the ordinal nature of this response variable, we explored the sensitivity of the results of model fitting to the assignment of scores in Figure 1. Specifically, we used normal and log-normal (the inverse to reflect the left-skewed nature of the distribution of forms) ridit scores (Agresti, 2010) to assign scores to the nine forms. We chose this method of analysis over ordinal logistic regression due to the sparsity of forms at certain time periods during the study.

Due to the timing of the 2009 fire (it occurred before our 2009 field assessments of large old trees), we could not fit a straightforward interaction of survey year and burn status at the site level. Our design for these two aspects is given by the following equation:

$$\mu_{ijt} = \beta_0 + \beta_1 D2005_{ijt} + \beta_2 D2009_{ijt} + \beta_3 D2012_{ijt} + \beta_4 D2015_{ijt} + \beta_5 F_{ijt} \times D2009_{ijt} \\ + \beta_6 F_{ijt} \times D2012_{ijt} + \beta_7 F_{ijt} \times D2015_{ijt} + site_i + tree_{ij}$$

where μ_{ijt} is the mean for tree j on site i at time point t ; $D2005_{ijt}$ is a dummy variable, which is 1 for year 2005 and 0 otherwise; F_{ijt} is 1 if the site experienced the 2009 wildfire and 0 otherwise; and $site_i$ and $tree_{ij}$ are random effects for the site and tree respectively.

This model specification (ignoring the random effects) is summarized in Table 1.

Table 1: Design structure for survey year and fire in modelling of pathways of decline of large old hollow-bearing trees.

Fire	1997	2005	2009	2012	2015
Unburned	β_0	$\beta_0 + \beta_1$	$\beta_0 + \beta_2$	$\beta_0 + \beta_3$	$\beta_0 + \beta_4$
Burned	β_0	$\beta_0 + \beta_1$	$\beta_0 + \beta_2$ + β_5	$\beta_0 + \beta_3$ + β_6	$\beta_0 + \beta_4 + \beta_7$

We used the leave one out cross validation information criteria (LOOIC) (Watanabe, 2010; Gelman *et al.*, 2014; Vehtari *et al.*, 2016) to choose the simplest model with two LOOIC units of the best fitting model among the 36 models listed in Appendix 1. We used the brms package (Bürkner, 2017) within the R computing environment (R Core Team, 2017) to complete our analysis. We used the default values in brms for all model parameters and ran four chains for 10000 iterations each omitting a burn-in of 2000 with a thinning factor of eight, giving 4000 posterior samples for inference. We assessed the mixing of the chain using the Rhat statistic of Gelman and Rubin (1992).

RESULTS

A total of 36 of our 96 long-term sites supported living trees at the outset of our investigation in 1997. Overall, 168 of the 534 hollow-bearing trees were alive when we first surveyed them in 1997. Table 2 shows the substantial rates of mortality of living trees, particularly on sites burned in 2009 with more than 60% of trees that were alive in 1997 having died 18 years later. Even on unburned sites, one-quarter of initially live trees in 1997 were dead by 2015 (Table 2a). We found evidence of deterioration in almost all trees that were surveyed; only ~4% of trees on sites burned in 2009 were in the same form in 2015 that they were when first measured in 1997. The equivalent value for unburned sites was higher (~15%) but nevertheless our data indicated that tree deterioration between 1997 and 2015 was substantial (Table 2b).

Table 2. Percentage rates of mortality of living trees and rates of deterioration in all trees relative to 1997 (the commencement of this study). Note the 2005 surveys pre-dates the major wildfires that occurred in 2009.

A. Mortality relative to 1997.

	2005	2009	2012	2015
Unburned sites	0%	13.9	20.5	25.0
Sites burned in 2009	0%	37.5	52.9	61.0

B. Tree deterioration relative to 1997. Rates of deterioration correspond to trees that moved through one or more forms (see Figure 1) to a more advanced stage of condition.

	2005	2009	2012	2015
Unburned sites	9.5%	74.8	81.7	84.8
Sites burned in 2009	9.5%	88.8	92.3	96.1

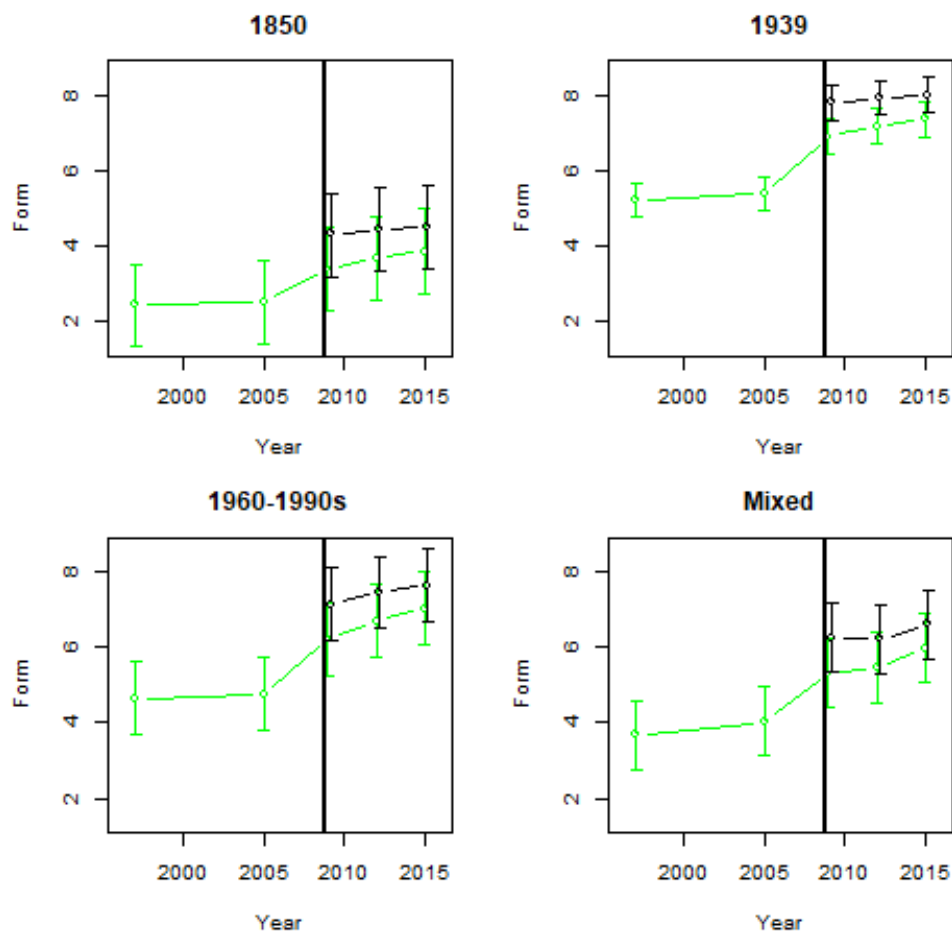
The best fitting statistical model derived from our analysis contained evidence of strong effects of survey year, stand age, and an interaction between survey year and stand age, fire at the site level, and the amount of fire in the surrounding landscape in 2009 (Appendix 1, Table S2). The best fitting models for the ridit scores (normal and inverse log-normal) were very similar in nature to the original scoring of tree form (see Figure 1 and Appendix 1, Figures S2-S3 and Tables S2-S4).

One of the most marked effects in our analysis was for stand age, with old growth stands (dating from ~ 1850) being characterized by trees in a much lower (more intact) form category than other age classes of forest we examined (Figure 2). The transitions of trees to more decayed forms over time also was less pronounced in old growth stands relative to the other age cohorts in our study, including the prolonged period preceding the 2009 fires (Figure 2). This difference was reflected by a stand age x year interaction indicating differences in tree decline pathways in stands of different age.

Our analyses revealed that fire in 2009 at the site level had major effects on tree decline with it markedly elevating the decay state of large old trees (to higher values of tree form) in all age cohorts of forest (Figure 2). The rate of decline also increased with an increasing amount of burned forest in the surrounding landscape. Relative to other age cohorts, the large old trees in old growth stands were in a much lower (more intact) form class at the outset of our investigation (in 1997) and remained so throughout the study (until 2015). Conversely, almost all trees in both the 1939 and the 1960-1990 age classes had progressed to the most advanced stages of decay (form class 8; see Figure 1) or had collapsed by 2015 (form class 9) (Figure 2). This was particularly the case on sites of these age classes that had been burned in the 2009 fire and where sites were characterized by a large amount of burned forest in the surrounding landscape.

Figure 2. Posterior means and 95% credible intervals of tree form by year of stand age origin and survey year. Unburned sites are indicated in green and burned in black and the 2009 wildfire is indicated by the vertical line. The amount of fire in the surrounding landscape is held fixed at the site mean. Note that trees of increasing form are

225 **increasingly decayed (see Figure 1).**



226

227 Although we found clear evidence for particular patterns of tree decline influenced by

228 factors like stand age and fire, our analyses also was characterized by strong random tree

229 effects ($SD = 1.81$) and strong random site effects ($SD = 1.42$) compared to a residual

230 standard deviation of 0.97. This indicated high levels of variability in decay among individual

231 trees and also substantial between-site variability in tree decline (Figure 2 and Appendix

232 Table S2).

233 DISCUSSION

234 We sought to quantify the extent and patterns of temporal decline in the condition of

235 large old trees and the factors affecting that decline in the Mountain Ash forests of south-

236 eastern Australia. Our empirical data underscored the fact that almost all trees had

deteriorated in condition in the 18 years of this study (Table 2). Indeed, almost no trees on burned sites remained in the same state as when first measured in 1997. Rates of deterioration on unburned sites also were substantial with a shift in condition state (see Figure 1) recorded in almost 85% of the 534 trees we measured. Some level of deterioration of trees in younger stands is part of the process of developing old-growth stand characteristics (Franklin *et al.*, 2002) such as patterns of vertical heterogeneity in canopy height (Brokaw and Lent, 1999). However, the rapid rate of deterioration in large old hollow-bearing trees in Mountain Ash forests that we have quantified indicates that very few stands will support large old trees that are a key part of stand structural complexity (*sensu* Lindenmayer and Franklin, 2002) and which are critical for a wide range of key ecosystem processes (Lindenmayer and Laurance, 2017).

We found evidence of pronounced rates of tree mortality, with more than 60% of live trees on burned sites dying during our study. This result was expected given that Mountain Ash trees are known to be highly sensitive to the effects of fire (Ashton, 1981; Lindenmayer, 2009a). However, the high rate of mortality of living trees on unburned sites was highly unexpected with a quarter of our measured population of living trees dying between 1997 and 2015 (Table 2a). The reasons for this result are not clear, but it is possible that the severe drought conditions and associated markedly elevated temperatures in our study region, particularly during the Millennium Drought (van Dijk *et al.*, 2013) triggered the death of many living trees. Drought stress has been well documented in large old living trees in a wide range of ecosystems (Choat *et al.*, 2012; Anderegg *et al.*, 2015; Lindenmayer and Laurance, 2017). However, drought does not fully account for our results given that tree death continued well after the Millennium Drought was broken, unless there were prolonged lag effects persisting in the ecosystem despite higher rainfall and lower maximum temperatures. Further work is needed to determine if lag effects occur in Mountain Ash (and other) forest

ecosystems. Irrespective of the underlying reasons for the high levels of tree mortality, our results are cause for considerable concern. This is because such large old living hollow-bearing trees should be long-lived (500+ years; Wood *et al.*, 2010) indicating that current rates of trees death will undermine populations of such keystone structures to levels of abundance below those needed to maintain key ecological functions such as the provision of suitable habitat for cavity-dependent biota (Lindenmayer and Sato, 2018).

Factors affecting tree decay

Our analysis highlighted how such factors as time, stand age and fire can individually and in combination, strongly affect the decay (and eventual collapse) of large old trees. In particular, we found compelling evidence that patterns of tree decline were markedly slower in old growth forest relative to the other three stand age classes we examined. We found evidence of a time x stand age interaction. Old growth forest was characterized by overall lower (i.e. less decayed) tree forms at the outset of our study in 1997. After accounting for different starting points for different tree forms in different aged stands, trees by the end of our investigation in 2015 trees in old growth forest were still less decayed than in younger stands (Figure 2). In addition, *rates* of tree deterioration were slower in old growth compared to younger-aged stands (Figure 2). This result was consistent irrespective of whether forest had been burned in 2009 or escaped being burned in that fire. Such patterns of retarded tree deterioration in old growth forest also characterized the years preceding as well as after wildfires in 2009.

Our analyses revealed that trees in older forest decayed less rapidly than trees of equivalent tree form in younger forests. At least two factors may explain this result. First, large old living trees in younger forests are typically biological legacies (*sensu* Franklin *et al.*, 2000) remaining after past disturbances like fire and logging (Lindenmayer, 2009b). Survival following past disturbances may compromise the integrity (and hence the standing life) of

these remaining trees leading to accelerated decline. For example, many living trees in young regrowth forest (that regenerated between 1960 and 1990) have fire scars as a result of damage by past fires and/or logging operations (Lindenmayer *et al.*, 1991). Second, several recent studies have shown that microclimatic conditions in old growth forests are markedly different to those in younger regrowth forest (Frey *et al.*, 2016) and can help dampen the effects of climate extremes on biota (Betts *et al.*, 2017). This may be particularly important for large old trees which can be particularly prone to elevated levels of mortality resulting from drought and high temperatures (Anderegg *et al.*, 2015; Lindenmayer and Laurance, 2017), such as experienced in the study area in several years over the period of our investigation. In this way, an old tree growing within a young stand may not survive such conditions whereas an old tree of equivalent form may undergo less deterioration if located within an old growth stand. This may explain, for example, why the interaction between stand age and year preceding the major wildfire in 2009 had less pronounced effects in old growth forest than in younger forests (Figure 2, Appendix Table S2).

We found evidence for a positive association between amount of burned forest in the landscape surrounding a site and deterioration of large old hollow-bearing trees (Appendix Table S2). The most likely reason for this finding is changes in wind movement when extensive stands of trees are damaged by fire such as the stand-replacing or partial stand-replacing conflagrations that characterize Mountain Ash forests. . Previous studies in Mountain Ash forests have revealed that hollow-bearing trees in retained linear strips are susceptible to windthrow when adjacent forest is clearcut (Lindenmayer *et al.*, 1997). The results of this new study suggest that changes in landscape cover associated with fire also can have major impacts on key ecosystem processes (McKenzie *et al.*, 2011) such as the decay of large old hollow-bearing trees.

A key pattern in our study was the rapid deterioration of large old trees in the youngest aged stands (*viz*: those regenerating after fires in 1939 and following disturbance between 1960 and 1990). In these forests, a very high proportion of large old trees were either in the most advanced state of tree decay (form 8) or had collapsed (form 9). This is a major concern given that 98.8% of the Mountain Ash forest ecosystem supports forest belonging to these age cohorts (or even younger). As the majority of the forest estate is 80 years old (or younger) and large old trees typically do not develop in Mountain Ash trees until they are at least 120-190 years old (Ambrose, 1982; Lindenmayer *et al.*, 2017), there is a strong chance that almost all of the existing population of large old trees may be lost from the vast majority of the Mountain Ash ecosystem before replacement trees of suitable age can develop. Hence, the ecosystem could be largely devoid of such keystone structures for 20-40 years and potentially somewhat longer.

Implications for forest management and protection

We have shown that the dynamics of tree decay is markedly different in old growth forest relative to other forest age cohorts in the Mountain Ash ecosystem. This underscores the critical importance of protecting old growth forests, especially as they are increasing rare globally (see Mackey *et al.*, 2015; Watson *et al.*, 2018). In the case of the Mountain Ash ecosystem, only 1.16% of the estate is currently old growth or 1/30th to 1/60th of what it was historically (Lindenmayer, 2017) and considerable effort will therefore be needed to significantly expand its spatial extent.

Whilst large old trees are in better condition and are more likely to persist in old growth Mountain Ash stands, it is also critically important to increase levels of protection for them elsewhere in the landscape. We suggest that the best way to protect these trees will be with buffers of uncut forest to shelter them from exposure such as elevated windspeeds and other factors that can accelerate their rate of decline (Lindenmayer *et al.*, 2013). Better

protection of these trees throughout Mountain Ash forests also will be critical for efforts to protect as range of cavity-tree dependent species that are of conservation concern such as Leadbeater's possum, greater glider and the yellow-bellied glider (Lindenmayer *et al.*, 2017). Deliberate killing of living trees may be an option to increase populations of dead trees and create habitat for cavity-dependent taxa in some ecosystems (e.g. Bull and Partridge, 1986). However, such actions will not be particularly effective in Mountain Ash forests because: (1) large old dead trees decay quickly (Lindenmayer *et al.*, 2016), (2) all existing large old living hollow-bearing trees need to be protected because of their comparatively long standing lives, and (3) small-diameter dead trees are unlikely to have the dimensions that make them suitable for occupancy by cavity-dependent species such as arboreal marsupials (Lindenmayer *et al.*, 2017).

Large old trees only become large and old by first being younger smaller trees and this indicates a need to extend forest protection strategies beyond a focus on old growth (where such trees are most abundant) (Lindenmayer *et al.*, 2000) to include extensive areas that are presently young forest but which have the potential, if left undisturbed, to eventually become new cohorts of much needed old growth forest. This is not a problem limited to Mountain Ash forests; it extends to many forest ecosystems globally where old growth forest is rare or absent and urgently needs to be restored (Watson *et al.*, 2018) as well as numerous environments where populations of large old trees are in decline (Lindenmayer and Laurance, 2017). A key challenge is to determine where in forest landscapes it is best to focus old growth stand and old growth tree protection. Previous environmental modelling in Mountain Ash landscapes indicates that old growth stands are most likely to develop including flat plateaux and deep south-facing valleys (Mackey *et al.*, 2002). Protection of these areas from disturbances such as logging should be prioritized. Finally, given the prolonged time required to recruit large old trees and stands of old growth in almost all forest ecosystems, there is a

361 clear need for very long-term planning to ensure the maintenance of populations of the large
362 old hollow-bearing trees that often characterize such areas.

363

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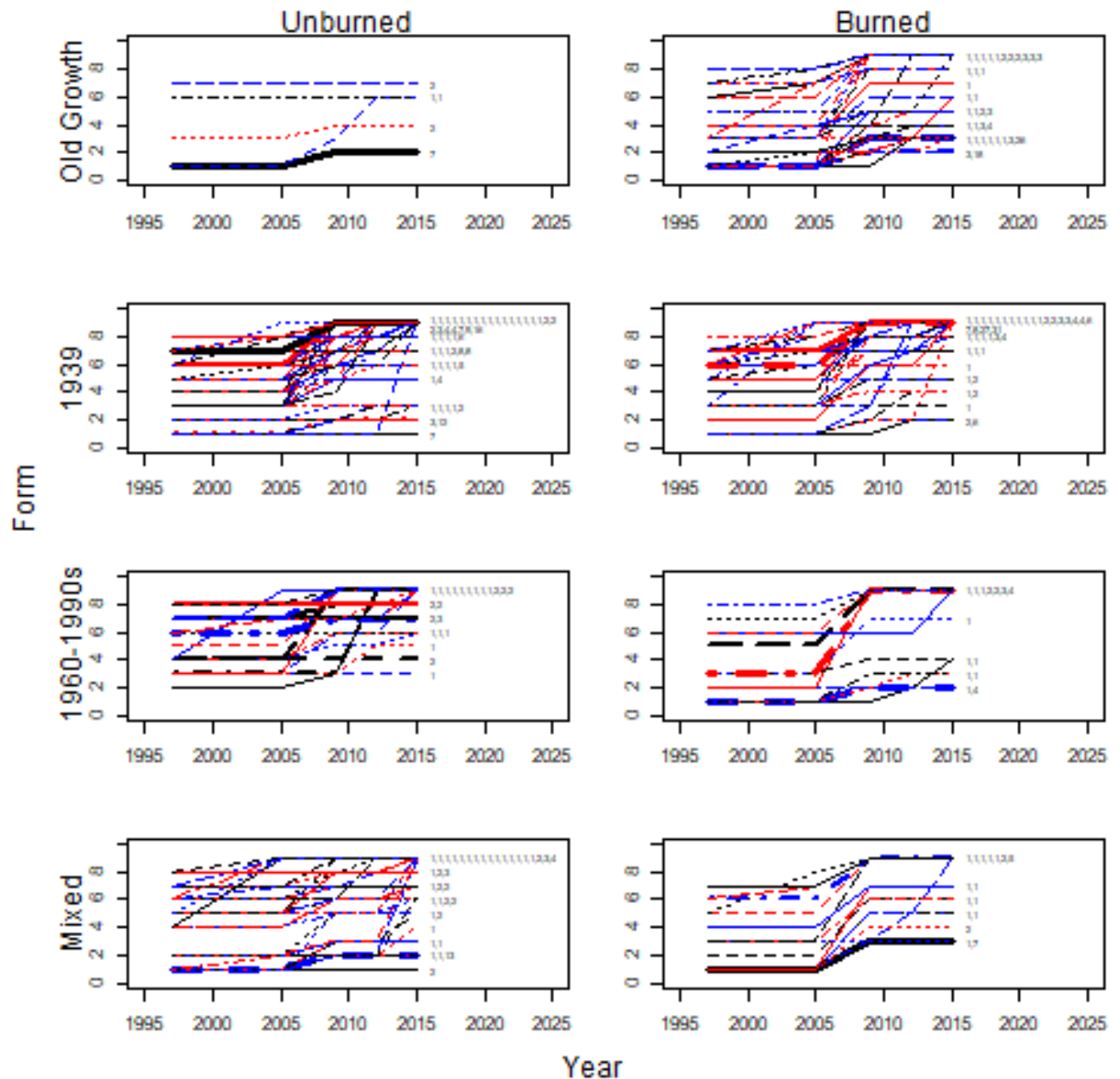
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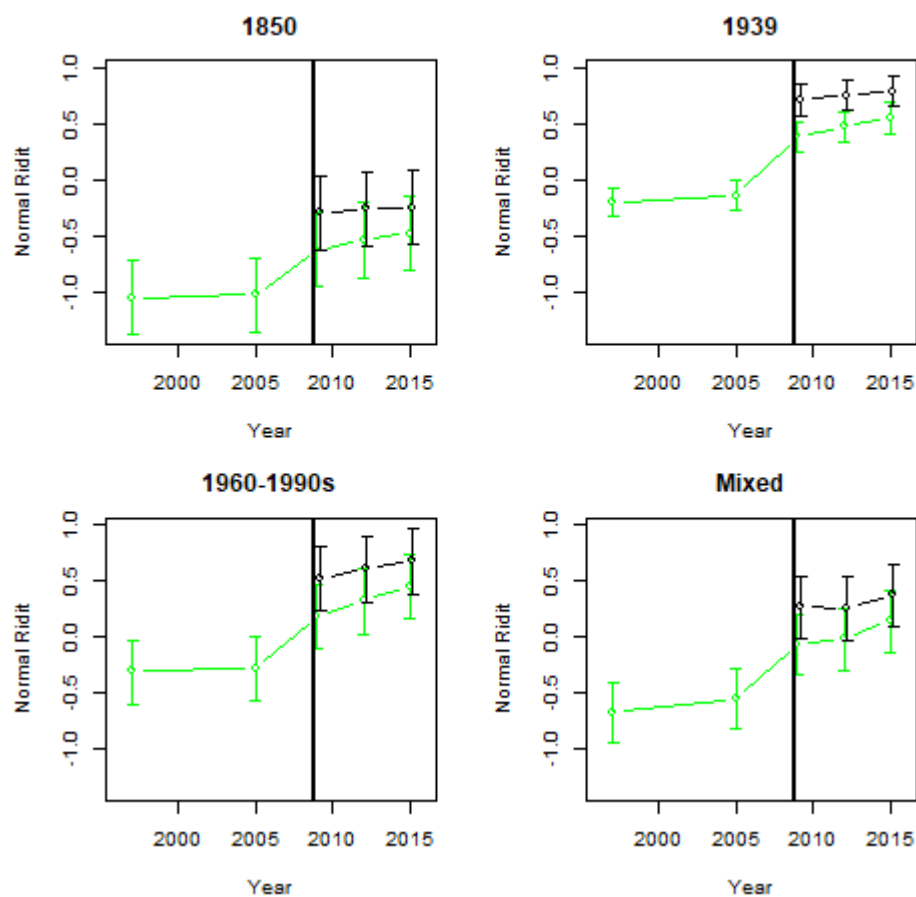
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APPENDICES

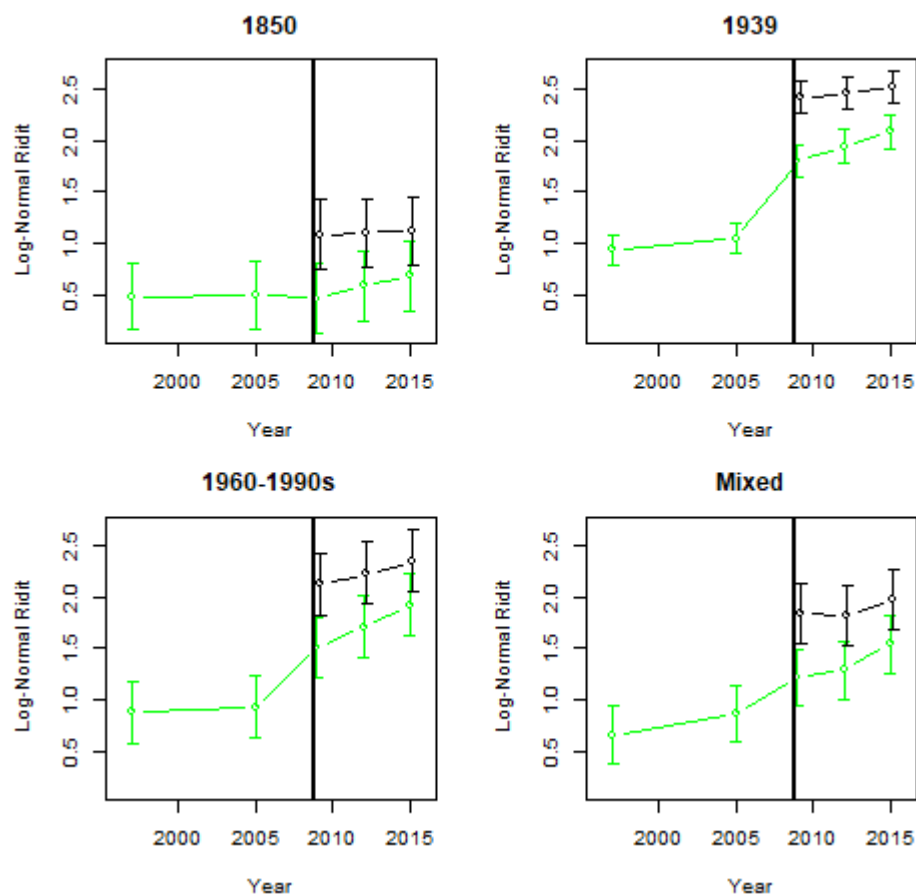
Appendix Figure S1: Individual trajectories of trees (as measured by form, see figure 1 in the manuscript) by stand age and burned status. The numbers to the right of each trajectory represent the number of trees that share the trajectory that ends in the given form, this is also indicated by the line thickness. For example, in the old growth burned panel, there are 11 trajectories that end in form 9 (collapse), 5 of which are single trees, 3 are shared by 2 trees and 3 by 3 trees and there is only 1 tree that ends in form 7.



514 **Appendix Figure S2: Posterior means and 95% credible intervals of normal riddit (see**
 515 **methods) by stand age. Unburned sites are indicated in green and burned in black and**
 516 **2009 wildfire is indicated by the vertical line. The amount of fire in the surrounding**
 517 **landscape is held fixed at the site mean.**



Appendix Figure S2: Posterior means and 95% credible intervals of log normal ridit (see methods) by stand age. Unburned sites are indicated in green and burned in black and 2009 wildfire is indicated by the vertical line. The amount of fire in the surrounding landscape is held fixed at the site mean.



Appendix Table 1: List of models considered. Where y2005D, y2009D, y2012D, y2015D are dummy variables for year, FA.y2009D, FA.y2012D, FA.y2015D are dummy variables for Fire at the site level in 2009 (see methods); StandAge is categorical variable with levels 1850, 1939, 1960-1990s and Mixed age; harvest.tvar is the time varying amount of harvesting in the surrounding landscape for each site; and fire.any.tvar is the amount of fire in the surrounding landscape due to the 2009 fire (note it is zero in 1997 and 2005). StandAge:(y2005D + y2009D + y2012D + y2015D) corresponds to the interaction between stand age survey year and StandAge:(FA.y2009D + FA.y2012D + FA.y2015D) represents the 3-way interaction between stand age and the site level fire in 2009 and survey year.

Nu mb er	Model
1	1+(1 SiteCode) + (1 TreeCode)
2	1 + y2005D + y2009D + y2012D + y2015D+(1 SiteCode) + (1 TreeCode)
3	1 + y2005D + y2009D + y2012D + y2015D + StandAge+(1 SiteCode) + (1 TreeCode)
4	1 + y2005D + y2009D + y2012D + y2015D + FA.y2009D + FA.y2012D + FA.y2015D+(1 SiteCode) + (1 TreeCode)
5	1 + y2005D + y2009D + y2012D + y2015D + harvest.tvar+(1 SiteCode) + (1 TreeCode)
6	1 + y2005D + y2009D + y2012D + y2015D + fire.any.tvar+(1 SiteCode) + (1 TreeCode)
7	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D+(1 SiteCode) + (1 TreeCode)
8	1 + y2005D + y2009D + y2012D + y2015D + StandAge+ harvest.tvar+(1 SiteCode) + (1 TreeCode)
9	1 + y2005D + y2009D + y2012D + y2015D + StandAge+ fire.any.tvar+(1 SiteCode) + (1 TreeCode)
10	1 + y2005D + y2009D + y2012D + y2015D + FA.y2009D + FA.y2012D + FA.y2015D+ harvest.tvar+(1 SiteCode) + (1 TreeCode)
11	1 + y2005D + y2009D + y2012D + y2015D + FA.y2009D + FA.y2012D + FA.y2015D+ fire.any.tvar+(1 SiteCode) + (1 TreeCode)
12	1 + y2005D + y2009D + y2012D + y2015D + harvest.tvar + fire.any.tvar+(1 SiteCode) + (1 TreeCode)
13	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+(1 SiteCode) + (1 TreeCode)
14	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D + fire.any.tvar+(1 SiteCode) + (1 TreeCode)
15	1 + y2005D + y2009D + y2012D + y2015D + StandAge + harvest.tvar + fire.any.tvar+(1 SiteCode) + (1 TreeCode)
16	1 + y2005D + y2009D + y2012D + y2015D + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+ fire.any.tvar+

	StandAge:(y2005D + y2009D + y2012D + y2015D)+(1 SiteCode) + (1 TreeCode)
33	1 + y2005D + y2009D + y2012D + y2015D + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+ fire.any.tvar+ (1 SiteCode) + (1 TreeCode)
34	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+ fire.any.tvar+(1 SiteCode) + (1 TreeCode)
35	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+ fire.any.tvar+ StandAge:(y2005D + y2009D + y2012D + y2015D)+(1 SiteCode) + (1 TreeCode)
36	1 + y2005D + y2009D + y2012D + y2015D + StandAge + FA.y2009D + FA.y2012D + FA.y2015D + harvest.tvar+ fire.any.tvar+ StandAge:(y2005D + y2009D + y2012D + y2015D) + StandAge:(FA.y2009D + FA.y2012D + FA.y2015D)+(1 SiteCode) + (1 TreeCode)

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Appendix Table S2: Model summary for Tree Form (model 29 from Appendix Table S1). We report the posterior mean, 95% credible intervals, effective sample size and the Gelman and Rubin Rhat statistic for each model parameter.

	Estimate	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	2.46	1.36	3.53	3635.58	1
y2005D	0.09	-0.16	0.35	3869.29	1
y2009D	0.73	0.4	1.05	3712.17	1
y2012D	1.01	0.68	1.34	4000	1
y2015D	1.19	0.86	1.53	4000	1
StandAge2.1939	2.75	1.57	3.91	3602.48	1
StandAge3.19601990s	2.18	0.73	3.59	3647.18	1
StandAge4.Mixed	1.21	-0.22	2.65	3673.78	1
FA.y2009D	0.92	0.67	1.15	3881.99	1
FA.y2012D	0.75	0.52	1	4000	1
FA.y2015D	0.63	0.4	0.87	4000	1
fire.any.tvar	0.73	0.45	1.01	4000	1
y2005D:StandAge2.1939	0.1	-0.2	0.4	3859.43	1
y2005D:StandAge3.19601990s	0.02	-0.42	0.46	3566.44	1
y2005D:StandAge4.Mixed	0.26	-0.12	0.63	3870.55	1
y2009D:StandAge2.1939	0.75	0.42	1.06	3701.81	1
y2009D:StandAge3.19601990s	0.61	0.16	1.05	3727.76	1
y2009D:StandAge4.Mixed	0.7	0.31	1.1	3862.02	1
y2012D:StandAge2.1939	0.73	0.42	1.05	4000	1
y2012D:StandAge3.19601990s	0.81	0.37	1.27	3850.93	1
y2012D:StandAge4.Mixed	0.55	0.16	0.94	3703.3	1
y2015D:StandAge2.1939	0.76	0.42	1.09	3880.24	1
y2015D:StandAge3.19601990s	0.94	0.49	1.39	3799.03	1
y2015D:StandAge4.Mixed	0.89	0.48	1.29	3604.24	1
Site Code SD	1.42	1.15	1.75	3384.26	1
Tree Code SD	1.81	1.69	1.94	3786.74	1
Residual SD	0.97	0.94	1	3934.6	1

Appendix Table S3: Model summary for Tree Form – normal ridits (model 29 from Appendix Table S1). We report the posterior mean, 95% credible intervals, effective sample size and the Gelman and Rubin Rhat statistic for each model parameter.

	Estimate	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	-1.05	-1.38	-0.72	3762.65	1
y2005D	0.03	-0.05	0.1	3843.5	1
y2009D	0.34	0.24	0.45	3675.46	1
y2012D	0.43	0.33	0.53	3786.86	1
y2015D	0.49	0.39	0.59	3823.82	1
StandAge2.1939	0.85	0.49	1.21	3820.98	1
StandAge3.19601990s	0.74	0.3	1.16	3813.98	1
StandAge4.Mixed	0.37	-0.05	0.8	3818.53	1
FA.y2009D	0.33	0.26	0.4	4000	1
FA.y2012D	0.28	0.2	0.35	4000	1
FA.y2015D	0.23	0.16	0.31	3744.09	1
fire.any.tvar	0.26	0.18	0.35	3822.99	1
y2005D:StandAge2.1939	0.04	-0.05	0.13	3713.45	1
y2005D:StandAge3.19601990s	0.01	-0.13	0.14	3954.81	1
y2005D:StandAge4.Mixed	0.1	-0.02	0.21	3875.14	1
y2009D:StandAge2.1939	0.16	0.06	0.26	3484.67	1
y2009D:StandAge3.19601990s	0.07	-0.07	0.21	4000	1
y2009D:StandAge4.Mixed	0.19	0.06	0.31	3829.91	1
y2012D:StandAge2.1939	0.16	0.07	0.26	3742.31	1
y2012D:StandAge3.19601990s	0.13	-0.01	0.26	4000	1
y2012D:StandAge4.Mixed	0.14	0.02	0.26	3872.83	1
y2015D:StandAge2.1939	0.18	0.08	0.28	3782.29	1
y2015D:StandAge3.19601990s	0.18	0.04	0.32	4000	1
y2015D:StandAge4.Mixed	0.25	0.12	0.37	3746.13	1
Site Code SD	0.42	0.34	0.52	3513.8	1
Tree Code SD	0.53	0.5	0.57	3808.58	1
Residual SD	0.3	0.29	0.3	4000	1

Appendix Table S4: Model summary for Tree Form – inverse log normal ridits (model 29 from Appendix Table S1). We report the posterior mean, stand error, 95% credible intervals, effective sample size and the Gelman and Rubin Rhat statistic for each model parameter.

	Estimate	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	0.48	0.16	0.8	3713.23	1
y2005D	0.02	-0.11	0.16	3885.56	1
y2009D	-0.06	-0.23	0.11	3964.92	1
y2012D	0.07	-0.1	0.24	3835.07	1
y2015D	0.16	0	0.33	4000	1
StandAge2.1939	0.46	0.1	0.81	3292.66	1
StandAge3.19601990s	0.4	-0.04	0.85	4000	1
StandAge4.Mixed	0.18	-0.25	0.6	3945.32	1
FA.y2009D	0.62	0.5	0.74	3820.5	1
FA.y2012D	0.52	0.4	0.64	3889.81	1
FA.y2015D	0.44	0.32	0.56	3631.17	1
fire.any.tvar	0.13	-0.02	0.27	3702.43	1
y2005D:StandAge2.1939	0.09	-0.07	0.24	3880.32	1
y2005D:StandAge3.19601990s	0.03	-0.21	0.25	3715.16	1
y2005D:StandAge4.Mixed	0.18	-0.01	0.38	3933.1	1
y2009D:StandAge2.1939	0.88	0.71	1.05	3898.61	1
y2009D:StandAge3.19601990s	0.65	0.41	0.89	3854.65	1
y2009D:StandAge4.Mixed	0.58	0.37	0.78	3919.51	1
y2012D:StandAge2.1939	0.9	0.74	1.07	4000	1
y2012D:StandAge3.19601990s	0.72	0.48	0.95	3919.39	1
y2012D:StandAge4.Mixed	0.53	0.33	0.73	4000	1
y2015D:StandAge2.1939	0.95	0.78	1.12	4000	1
y2015D:StandAge3.19601990s	0.83	0.6	1.06	3793.7	1
y2015D:StandAge4.Mixed	0.68	0.48	0.88	4000	1
Site Code SD	0.39	0.3	0.49	3656.41	1
Tree Code SD	0.59	0.55	0.64	3768.11	1
Residual SD	0.5	0.48	0.51	4000	1

Appendix Table S5: Pairwise comparisons for Tree Form, Tree-form normal ridits and inverse log normal ridits by survey year, stand age and burned status For example, line 1 compares 1939 to old growth forest in 1997 unburned forest and by contrast line 11, compares the differences between 2005 and 1997 in old growth and 1939 regrowth unburned forest. We present point estimates (posterior means) and 95% credible limits (labeled as LCL and UCL). Note that the time varying covariate, amount of fire in the surrounding landscape has been held fixed at the mean value for the given year(s).

Survey Year	Stand Age	Burned	Form 1-9			Form – normal ridits			Form inverse log normal ridits		
			Est	LCL	UCL	Est	LCL	UCL	Est	LCL	UCL
1997	1939-OG	N	2.75	1.57	3.91	0.85	0.49	1.21	0.46	0.1	0.81
1997	19601990s-OG	N	2.18	0.73	3.59	0.74	0.3	1.16	0.4	-0.04	0.85
1997	Mixed-OG	N	1.21	-0.22	2.65	0.37	-0.05	0.8	0.18	-0.25	0.6
1997	19601990s-1939	N	-0.57	-1.61	0.5	-0.11	-0.43	0.19	-0.06	-0.39	0.27
1997	Mixed-1939	N	-1.54	-2.53	-0.56	-0.48	-0.78	-0.18	-0.28	-0.59	0.05
1997	Mixed-19601990s	N	-0.97	-2.28	0.35	-0.37	-0.76	0.02	-0.22	-0.64	0.18
2005-1997	OG	N	0.09	-0.16	0.35	0.03	-0.05	0.1	0.02	-0.11	0.16
2005-1997	1939	N	0.2	0.04	0.36	0.06	0.01	0.11	0.11	0.02	0.19
2005-1997	19601990s	N	0.11	-0.25	0.46	0.03	-0.08	0.14	0.05	-0.14	0.23
2005-1997	Mixed	N	0.35	0.06	0.63	0.12	0.04	0.21	0.21	0.06	0.35
2005-1997	1939-OG	N	0.1	-0.2	0.4	0.04	-0.05	0.13	0.09	-0.07	0.24
2005-1997	19601990s-OG	N	0.02	-0.42	0.46	0.01	-0.13	0.14	0.03	-0.21	0.25
2005-1997	Mixed-OG	N	0.26	-0.12	0.63	0.1	-0.02	0.21	0.18	-0.01	0.38
2005-1997	19601990s-1939	N	-0.08	-0.48	0.3	-0.03	-0.15	0.08	-0.06	-0.26	0.15
2005-1997	Mixed-1939	N	0.15	-0.17	0.47	0.06	-0.04	0.16	0.1	-0.07	0.26
2005-1997	Mixed-19601990s	N	0.24	-0.21	0.69	0.09	-0.05	0.23	0.16	-0.08	0.4
2009-2005	OG	N	0.85	0.54	1.16	0.4	0.3	0.49	-0.04	-0.21	0.13
2009-2005	1939	N	1.5	1.29	1.71	0.52	0.45	0.58	0.75	0.65	0.86
2009-2005	19601990s	N	1.45	1.07	1.81	0.46	0.35	0.58	0.58	0.38	0.77
2009-2005	Mixed	N	1.3	1.02	1.58	0.49	0.4	0.58	0.35	0.2	0.51
2009-2005	1939-OG	N	0.64	0.33	0.95	0.12	0.02	0.22	0.79	0.63	0.96
2009-2005	19601990s-OG	N	0.59	0.16	1.05	0.07	-0.07	0.21	0.62	0.39	0.86
2009-2005	Mixed-OG	N	0.44	0.06	0.83	0.09	-0.03	0.21	0.39	0.19	0.6
2009-2005	19601990s-1939	N	-0.05	-0.44	0.34	-0.06	-0.17	0.06	-0.17	-0.37	0.02
2009-2005	Mixed-1939	N	-0.2	-0.52	0.12	-0.03	-0.13	0.07	-0.4	-0.58	-0.23
2009-2005	Mixed-19601990s	N	-0.15	-0.6	0.29	0.02	-0.12	0.16	-0.23	-0.46	0.02
2012-2009	OG	N	0.29	-0.05	0.63	0.09	-0.01	0.19	0.13	-0.05	0.31
2012-2009	1939	N	0.27	0.07	0.48	0.09	0.03	0.15	0.14	0.03	0.25
2012-2009	19601990s	N	0.49	0.12	0.86	0.14	0.02	0.26	0.2	0	0.39
2012-2009	Mixed	N	0.14	-0.15	0.42	0.05	-0.05	0.13	0.08	-0.07	0.23
2012-2009	1939-OG	N	-0.02	-0.33	0.29	0	-0.09	0.1	0.02	-0.15	0.18
2012-2009	19601990s-OG	N	0.2	-0.26	0.65	0.06	-0.08	0.19	0.07	-0.16	0.31
2012-2009	Mixed-OG	N	-0.15	-0.56	0.24	-0.04	-0.16	0.09	-0.05	-0.26	0.16
2012-2009	19601990s-1939	N	0.22	-0.18	0.61	0.05	-0.07	0.17	0.05	-0.14	0.25
2012-2009	Mixed-1939	N	-0.14	-0.45	0.19	-0.04	-0.14	0.05	-0.07	-0.24	0.1
2012-2009	Mixed-19601990s	N	-0.35	-0.81	0.1	-0.1	-0.24	0.05	-0.12	-0.36	0.12
2015-2012	OG	N	0.18	-0.16	0.52	0.06	-0.04	0.17	0.1	-0.07	0.27
2015-2012	1939	N	0.21	0	0.41	0.08	0.02	0.15	0.15	0.04	0.25
2015-2012	19601990s	N	0.31	-0.07	0.67	0.12	0	0.23	0.21	0.02	0.4
2015-2012	Mixed	N	0.52	0.24	0.8	0.16	0.08	0.25	0.25	0.1	0.4
2015-2012	1939-OG	N	0.03	-0.28	0.34	0.02	-0.08	0.12	0.05	-0.11	0.21
2015-2012	19601990s-OG	N	0.13	-0.33	0.59	0.06	-0.09	0.2	0.11	-0.12	0.34
2015-2012	Mixed-OG	N	0.34	-0.06	0.75	0.1	-0.02	0.23	0.15	-0.05	0.36
2015-2012	19601990s-1939	N	0.1	-0.29	0.5	0.03	-0.09	0.16	0.06	-0.14	0.26
2015-2012	Mixed-1939	N	0.31	-0.01	0.63	0.08	-0.02	0.18	0.1	-0.07	0.27
2015-2012	Mixed-19601990s	N	0.21	-0.24	0.67	0.05	-0.1	0.19	0.04	-0.19	0.27

2009-2005	OG	Y	0.45	0.11	0.79	0.18	0.08	0.28	0.4	0.22	0.57
2009-2005	1939	Y	0.44	0.17	0.69	0.16	0.08	0.24	0.33	0.2	0.46
2009-2005	19601990s	Y	0.12	-0.3	0.54	0.07	-0.06	0.19	0.22	0	0.43
2009-2005	Mixed	Y	0.26	-0.1	0.61	0.12	0.01	0.23	0.29	0.11	0.47
2009-2005	1939-OG	Y	-0.01	-0.33	0.3	-0.02	-0.12	0.07	-0.07	-0.23	0.09
2009-2005	19601990s-OG	Y	-0.33	-0.78	0.14	-0.11	-0.25	0.03	-0.18	-0.42	0.05
2009-2005	Mixed-OG	Y	-0.18	-0.59	0.22	-0.06	-0.19	0.06	-0.1	-0.32	0.1
2009-2005	19601990s-1939	Y	-0.31	-0.72	0.08	-0.09	-0.21	0.03	-0.11	-0.31	0.09
2009-2005	Mixed-1939	Y	-0.17	-0.51	0.15	-0.04	-0.14	0.06	-0.04	-0.2	0.13
2009-2005	Mixed-19601990s	Y	0.14	-0.33	0.59	0.05	-0.09	0.2	0.08	-0.16	0.31
2012-2009	OG	Y	0.12	-0.14	0.38	0.04	-0.04	0.12	0.03	-0.11	0.16
2012-2009	1939	Y	0.11	-0.09	0.31	0.04	-0.03	0.1	0.04	-0.06	0.15
2012-2009	19601990s	Y	0.32	-0.07	0.71	0.09	-0.03	0.21	0.1	-0.1	0.29
2012-2009	Mixed	Y	-0.03	-0.35	0.3	-0.01	-0.11	0.1	-0.02	-0.2	0.15
2012-2009	1939-OG	Y	-0.02	-0.33	0.29	0	-0.09	0.1	0.02	-0.15	0.18
2012-2009	19601990s-OG	Y	0.2	-0.26	0.65	0.06	-0.08	0.19	0.07	-0.16	0.31
2012-2009	Mixed-OG	Y	-0.15	-0.56	0.24	-0.04	-0.16	0.09	-0.05	-0.26	0.16
2012-2009	19601990s-1939	Y	0.22	-0.18	0.61	0.05	-0.07	0.17	0.05	-0.14	0.25
2012-2009	Mixed-1939	Y	-0.14	-0.45	0.19	-0.04	-0.14	0.05	-0.07	-0.24	0.1
2012-2009	Mixed-19601990s	Y	-0.35	-0.81	0.1	-0.1	-0.24	0.05	-0.12	-0.36	0.12
2015-2012	OG	Y	0.06	-0.2	0.32	0.01	-0.06	0.09	0.01	-0.11	0.14
2015-2012	1939	Y	0.09	-0.12	0.29	0.04	-0.03	0.1	0.06	-0.04	0.17
2015-2012	19601990s	Y	0.18	-0.2	0.58	0.07	-0.05	0.19	0.12	-0.07	0.32
2015-2012	Mixed	Y	0.4	0.08	0.72	0.12	0.02	0.22	0.17	-0.01	0.34
2015-2012	1939-OG	Y	0.03	-0.28	0.34	0.02	-0.08	0.12	0.05	-0.11	0.21
2015-2012	19601990s-OG	Y	0.13	-0.33	0.59	0.06	-0.09	0.2	0.11	-0.12	0.34
2015-2012	Mixed-OG	Y	0.34	-0.06	0.75	0.1	-0.02	0.23	0.15	-0.05	0.36
2015-2012	19601990s-1939	Y	0.1	-0.29	0.5	0.03	-0.09	0.16	0.06	-0.14	0.26
2015-2012	Mixed-1939	Y	0.31	-0.01	0.63	0.08	-0.02	0.18	0.1	-0.07	0.27
2015-2012	Mixed-19601990s	Y	0.21	-0.24	0.67	0.05	-0.1	0.19	0.04	-0.19	0.27
2009-2005	OG	Y-N	-0.4	-0.83	0.03	-0.22	-0.35	-0.08	0.44	0.21	0.66
2009-2005	1939	Y-N	-1.06	-1.42	-0.7	-0.36	-0.48	-0.25	-0.43	-0.61	-0.24
2009-2005	19601990s	Y-N	-1.32	-1.79	-0.85	-0.39	-0.54	-0.25	-0.36	-0.6	-0.12
2009-2005	Mixed	Y-N	-1.03	-1.44	-0.63	-0.37	-0.49	-0.24	-0.06	-0.27	0.14
2009-2005	1939-OG	Y-N	-0.65	-0.98	-0.33	-0.14	-0.24	-0.05	-0.86	-1.03	-0.7
2009-2005	19601990s-OG	Y-N	-0.92	-1.4	-0.46	-0.18	-0.31	-0.04	-0.8	-1.03	-0.57
2009-2005	Mixed-OG	Y-N	-0.63	-1.02	-0.24	-0.15	-0.27	-0.02	-0.5	-0.7	-0.29
2009-2005	19601990s-1939	Y-N	-0.26	-0.67	0.13	-0.03	-0.15	0.09	0.06	-0.14	0.26
2009-2005	Mixed-1939	Y-N	0.03	-0.3	0.34	0	-0.11	0.1	0.37	0.2	0.53
2009-2005	Mixed-19601990s	Y-N	0.29	-0.17	0.75	0.03	-0.12	0.17	0.3	0.08	0.53

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